

Oceanographic influences on the dive behavior of juvenile loggerhead turtles (*Caretta caretta*) in the North Pacific Ocean

Evan A. Howell · Peter H. Dutton ·
Jeffrey J. Polovina · Helen Bailey ·
Denise M. Parker · George H. Balazs

Received: 4 August 2009 / Accepted: 22 December 2009
© US Government 2010

Abstract Satellite telemetry data from 17 juvenile loggerhead turtles (43.5–66.5 cm straight carapace length) were used in conjunction with oceanographic data to analyze the influence of regional and seasonal oceanography on dive behavior in the North Pacific Ocean. Combined dive behavior for all individuals showed that turtles spent more than 80% of their time at depths <5 m, and more than 90% of their time at depths <15 m. Multivariate classifications of dive data revealed four major dive types, three representing deeper, longer dives, and one representing shallower dives shorter in duration. Turtles exhibited variability in these dive types across oceanographic regions, with deeper, longer dives in the Hawaii longline swordfish fishing grounds during the first quarter of the year, as well as in the Kuroshio Extension Bifurcation Region and the region near the Baja California Peninsula, Mexico. Turtles in the Kuroshio Extension Bifurcation Region also exhibited dive variability associated with mesoscale eddy

features, with turtles making deeper, longer dives while associated with the strongest total kinetic energy. Turtles in the central North Pacific exhibited seasonality in dive behavior that appeared to reflect synchronous latitudinal movements with the North Pacific Subtropical Front and the associated seasonal, large-scale oceanography. Turtles made deeper, longer dives during the first quarter of the year within this region, the reported time and area where the highest loggerhead bycatch occurs by the longline fishery. These results represent the first comprehensive study of dive data for this species in this region. The increased understanding of juvenile loggerhead dive behavior and the influences of oceanography on dive variability should provide further insight into why interactions with longline fisheries occur and suggest methods for reducing the bycatch of this threatened species.

Communicated by R. Lewison.

E. A. Howell (✉) · J. J. Polovina · G. H. Balazs
Pacific Islands Fisheries Science Center, NOAA Fisheries,
2570 Dole Street, Honolulu, HI 96822-2396, USA
e-mail: Evan.Howell@noaa.gov

P. H. Dutton
Southwest Fisheries Science Center, NOAA Fisheries,
3333 North Torrey Pines Court, La Jolla, CA 92037-1022, USA

H. Bailey
Environmental Research Division, NOAA Fisheries,
1352 Lighthouse Avenue, Pacific Grove, CA 93950-2097, USA

D. M. Parker
Joint Institute for Marine and Atmospheric Research,
University of Hawaii, 1000 Pope Road,
Honolulu, HI 96822, USA

Introduction

Loggerhead turtles (*Caretta caretta*) are a threatened species widely distributed throughout temperate ocean basins. In the Pacific, loggerheads generally consist of two distinct genetic stocks; a North Pacific stock originating from breeding sites in Japan summarized in Kamezaki et al. (2003), and a South Pacific stock originating from breeding sites in Australia and New Caledonia (Bowen et al. 1995; Bowen and Karl 2007). The North Pacific stock inhabits foraging and developmental areas in coastal neritic and oceanic habitat all the way to the northeast Pacific off the coast of the Baja California Peninsula (BCP), Mexico (Bowen et al. 1995; Kamezaki and Matsui 1997; Peckham et al. 2007). Similarly, foraging and developmental habitat for the South Pacific breeding stock extends across the South Pacific, including offshore areas of the South

America coastline (Alfaro-Shigueto et al. 2004; Donoso and Dutton 2008; Boyle et al. 2009). Advances in satellite transmitter technologies over recent years have allowed researchers to collect geospatial information on loggerheads in various coastal and oceanic regions. These data have provided important information on turtle ecology that, among other things, have provided a means to elucidate migration patterns during early life stages (Bentivegna 2002; Dodd and Byles 2003; Hatase et al. 2007; Alfaro Shigueto et al. 2008). According to previous results in the North Pacific Ocean, the oceanic phase of a juvenile loggerhead may last a decade or more. During this phase, loggerheads migrate and forage along convergent fronts of temperature and productivity that span the entire North Pacific Ocean (Polovina et al. 2000, 2004; Kobayashi et al. 2008) in a region defined as the North Pacific Transition Zone (NPTZ) (Roden 1991; Polovina et al. 2001; Seki et al. 2002). Important small-scale habitat features (hotspots) also occur along this migratory pathway, with the Kuroshio Extension Bifurcation Region (KEBR) identified as an important habitat area for juvenile loggerheads (Polovina et al. 2006). These two regions have specific oceanographic characteristics. The KEBR lies west of 180° and has been identified as a dynamic area with intense mesoscale variability (Qiu 2001). The NPTZ is a region defined by strong physical and biological gradients that separate the oligotrophic North Pacific Subtropical Gyre (NPSTG) located to the south from the cold productive North Pacific Subarctic Gyre (NPSAG) located to the north (Roden 1980; Pickard and Emery 1990; Seki et al. 2002; Seki 2003). The southern edge of the NPTZ is bounded by the North Pacific Subtropical Frontal Zone (NPSTFZ), which contains multiple fronts and microfronts (Seki 2003). The NPSTFZ also contains the Transition Zone Chlorophyll Front (TZCF), an important migration and forage pathway for many pelagic animals (Polovina et al. 2001) associated with the 18°C isotherm in the central North Pacific (Bograd et al. 2004).

The NPTZ, specifically the NPSTFZ to the south, has historically been used by the Hawaii-based pelagic longline fishery to target swordfish (*Xiphias gladius*) north of Hawaii during the first half of the year (Seki et al. 2002). Large frontal features within the NPSTFZ can be represented by specific isotherms, e.g., the 17°C isotherm identifies the convergent Subtropical Front (STF) (Roden 1972, 1980; Seki 2003). During this period of the year, specifically January–March, interactions between the fishery and loggerheads may occur. Previous research on the sea surface temperature (SST) range of the Hawaii-based swordfish fleet showed that in the first quarter of the year they target a specific range centered near 18°C (Howell et al. 2008), which is the isotherm associated with the TZCF in this region. Tracking studies have shown that loggerheads were also associated with this region during

this time; turtles in two studies in the North Pacific were associated with the TZCF (Polovina et al. 2001, 2004) and turtles in another study additionally showed a strong association with the 17°C isotherm (Polovina et al. 2000).

The spatial overlap between the fishery and loggerhead presence results in bycatch interactions (Howell et al. 2008). These are statistically classified as rare events (McCracken 2004), yet the bycatch of juvenile loggerheads by longliners is a serious concern and United States federally mandated requirements attempt to minimize loggerhead bycatch. A recent spatial study on the historical bycatch of loggerheads by this fishery showed that the majority of interactions occurred within a specific SST range (Howell et al. 2008).

Dive behavior has been reported for loggerheads in various regions of the world's oceans (Sakamoto et al. 1990; Renaud and Carpenter 1994; Sato et al. 1994; Minamikawa 2000; Hays et al. 2002; Houghton et al. 2002; Godley et al. 2003), but only for two juvenile loggerheads in the central North Pacific Ocean where United States and other longline fisheries operate (Polovina et al. 2003, 2004). The possible importance of thermal niches for turtles has been hypothesized (Hays et al. 2002; McMahon and Hays 2006), and the importance of the 15°C isotherm as a thermal limit has been discussed for loggerheads and leatherbacks (McMahon and Hays 2006; Brazner and McMillan 2008). The ability to determine the influence of oceanography on loggerhead dive behavior is additionally important in understanding bycatch patterns, as spatio-temporal dive variability by loggerheads may change the possible vertical overlap between loggerheads and shallow set longline fishing gear.

We provide dive information from 17 juvenile loggerheads equipped with satellite-linked depth recorders (SDRs) in the central North Pacific Ocean. This represents the first comprehensive data set on dive behavior for loggerheads in this important region. We analyze the variability in recorded dive behavior within three distinct regions of the North Pacific to identify spatiotemporal similarity and/or variability in movements and dive behavior. The geospatial information from several of these tracks has been used in a previous study, which included a description of the spatial association of one turtle in the KEBR with a warm-core eddy event (Polovina et al. 2006). Here, we expand on the previous results by including the dive information for this tag as well as tags from additional turtles that entered the KEBR region. These results will aid in our understanding of juvenile loggerhead dive behavior during their oceanic phase. An increased understanding of potential effects of oceanography on loggerhead dive behavior should assist in future conservation and bycatch studies working toward the reduction of loggerheads by longline fisheries in the North Pacific.

Methods

Study area and turtle tagging

Seventeen loggerhead turtles were equipped with Wildlife Computers, Inc. (Redmond, WA) model SDR-10 ($n = 3$) and SDR-16 ($n = 14$) Argos-linked satellite transmitters (hereupon referred to as tags) to provide geospatial location and dive information. The geospatial information and attachment methods from 6 of the 17 tags used in this study have been previously reported without dive information (Polovina et al. 2006). All 17 loggerheads in this study were incidentally caught during 2002–2004 by Long Beach, California-based longline vessels operating in the central North Pacific Ocean (Table 1). All of the turtles were juveniles and ranged in size from 44 to 66.5 cm straight carapace length (SCL). At capture, the hooking condition was noted and classified as follows: (1) lightly hooked (LH), if the turtle was only externally hooked in the fishing gear and did not swallow the hook; or (2) deeply hooked (DH), if the turtle swallowed the hook. Lightly hooked turtles were unhooked and released, while deeply hooked turtles were released with the hook and wire in the animal but with the monofilament leader cut close to the turtle's mouth following the guidelines set in Balazs et al. (1995). Turtles were outfitted with satellite tags attached to the carapace using the procedures outlined by Balazs et al. (1996). All turtles actively swam away or dove on release.

Data on daily locations of the turtles were determined from the signals received by Argos receivers on NOAA satellites. The accuracy of each position was estimated by Argos as a function of Doppler-shift in the frequency of the satellite tag and the number of transmissions received. Raw geographic positions for each individual track were filtered using a switching state-space model (Jonsen et al. 2007). The state-space model incorporates stages for both the observation error (satellite locations) and the movement dynamics (Jonsen et al. 2007; Bailey et al. 2008). Post-filtered data were then checked to ensure that no records were retained with speeds greater than 2.5 km h^{-1} . This final set of spatial data contained a daily geolocation for each individual based on the mean position estimate derived from the state-space model.

The study site was divided into three previously defined regions, the KEBR, the Hawaii-based Longline Swordfish Fishing Grounds (HLSFG), and the California Current (CC) (Fig. 1). The KEBR has been previously defined as the area to the west of the date line from approximately 155°E to 180° and between 30° and 40°N (Qiu 2001). The KEBR is a dynamic region characterized by warm-core and cold-core eddies as a result of meanders in the Kuroshio Extension Current (KEC) (Qiu 2001; Polovina et al. 2006). The HLSFG have been previously defined based on historical effort as the region between the KEBR and 140°W (Seki et al. 2002) and is characterized by three subregions: the oligotrophic NPSTG,

Table 1 Deployment and final transmission dates for satellite tags attached to juvenile loggerhead turtles during 2002–2004 with the transmitter duration from tag deployment to the end of transmission, the straight-line (SL) distance traveled during this period, the hooking classification and size

Dates			Duration (days)	Longitude		Latitude		SL distance (km)	Hook class	SCL (cm)
Tag	Start	End		Start	End	Start	End			
16129	09/05/2003	07/07/2005	484	133.19°W	153.62°W	35.60°N	36.36°N	1,854.54	DH	61
16131	11/03/2003	07/11/2004	252	140.24°W	173.49°W	37.72°N	36.47°N	2,936.82	LH	57
21128	02/18/2003	04/19/2004	427	155.18°W	170.39°E	31.11°N	31.64°N	3,255.48	DH	65.4
21130	02/18/2003	09/17/2004	578	149.82°W	157.82°W	31.69°N	40.09°N	1,178.6	LH	46
21138	02/16/2003	09/27/2003	224	149.77°W	168.32°W	31.80°N	37.48°N	1,806.91	DH	44
21411	09/03/2003	04/08/2004	219	132.16°W	175.08°W	35.06°N	30.99°N	3,996.32	LH	62.5
21412	09/10/2003	11/12/2004	430	133.00°W	171.34°E	34.54°N	34.44°N	5,032.84	DH	56.5
22277	01/04/2003	08/22/2003	231	139.00°W	164.10°W	32.91°N	37.78°N	2,332.41	DH	43.5
22328	10/14/2002	09/07/2003	329	140.24°W	175.53°E	41.33°N	40.59°N	3,673.99	LH	55.5
22329	12/27/2002	08/27/2003	244	140.91°W	162.59°W	34.48°N	37.24°N	1,973.25	LH	45.5
24644	04/09/2003	06/27/2004	446	161.06°W	168.87°E	29.94°N	38.91°N	2,916.75	LH	56.5
24645	11/17/2003	12/11/2004	391	150.14°W	166.91°E	37.25°N	38.17°N	3,745.32	DH	66.5
24646	01/08/2004	07/27/2004	202	154.28°W	172.29°W	32.90°N	34.24°N	1,673.05	LH	56
44359	01/08/2004	06/27/2004	172	154.64°W	177.65°W	33.74°N	35.93°N	2,109.23	DH	61
44360	01/07/2004	08/19/2004	226	155.43°W	178.29°W	33.15°N	41.10°N	2,202.52	DH	59.5
44361	01/11/2004	11/06/2004	301	155.83°W	175.45°W	32.52°N	34.81°N	1,830.53	LH	53.5
44362	02/10/2004	03/31/2004	51	151.99°W	154.26°W	31.64°N	32.70°N	244.01	DH	49

DH deeply hooked, LH lightly hooked, SCL straight carapace length

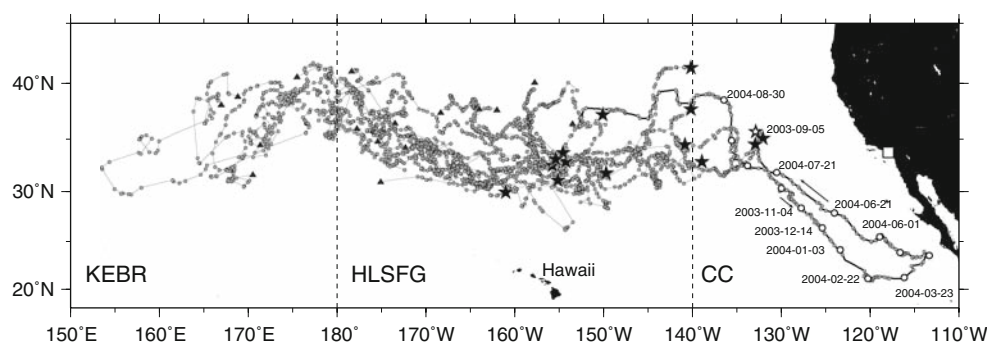


Fig. 1 Movements of 17 juvenile loggerhead turtles after release from longline fishing gear with annotation of the defined study areas: The Kuroshio extension bifurcation region (KEBR), the Hawaii Longline Swordfish Fishing Grounds (HLSFG), and the California Current (CC) region. Stars indicate release points. Triangles indicate

final transmission locations of individuals. The white square represents the Long Beach point of origin for the California-based longline fishery. Dates and white circles indicate representative locations for turtle 16129 within the CC region

the productive NPSAG, and the seasonally migrating NPTZ between them (Roden 1980). Finally, the CC region is then defined as the area to the east of 140°W.

Dive information was collected by the tags and transmitted to Argos receivers onboard NOAA satellites. Transmitters were pre-programmed to recognize an individual dive event, defined by the tag as the period between an initial vertical movement below 1 m and the first time the tag's saltwater switch indicated a return to the surface. Raw dive and time data were collected as frequency histograms by the transmitters based on predefined depth and duration bins programmed into the transmitter prior to deployment. These histograms were aggregated over four 6-h periods binned in specific depth or time intervals. All 17 tags were programmed with the same configurations for the dive-depth and dive-duration bins. The lower ranges of the depth bins (in meters) for the dive-depth distributions were 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 100, 150, and >150. The lower ranges of the duration bins (in minutes) for the dive-duration distributions were 2, 5, 10, 20, 30, 45, 60, 75, 90, 105, 120, 180, 240, and >240. The time-at-depth bins for the SDR-10 and SDR-16 models were programmed with different depth criteria. The lower ranges of the depth bins (m) for the time-at-depth distributions collected by the three initially deployed SDR-10 tags were 0, 5, 10, 15, 25, 35, 50, 60, 75, 100, 125, 150, 200, and >200. Initial collection and preliminary inspection of these reported data resulted in a modification of the programmed time-at-depth bins to capture the depth regions with the greatest activity. The lower ranges of the depth bins (m) for the time-at-depth distributions collected by the 14 subsequently deployed SDR-16 tags were 1, 5, 10, 15, 20, 25, 30, 40, 50, 60, 80, 100, 150, and >150. As a result of minimal crossover in the time-at-depth bins between the SDR-10 and SDR-16 tags, only the dive-depth and dive-duration information was pooled across all 17 tags. Time-at-depth dive information was only pooled for the SDR-16 tags

($n = 14$). All 17 tags were programmed to tabulate the collected dive information into 6-h periods prior to transmission to Argos receivers. These periods were programmed to correspond to Hawaii Standard Time as 2100–0300, 0300–0900, 0900–1500, and 1500–2100 h. These reflected midnight, dawn, mid-day, and dusk periods, respectively. Data were compiled from electronic information received from Argos for each transmitter ID. Data were converted to tabular form using the latest available version of SATPAK30 (Wildlife Computers, Inc. Redmond, WA). Time-at-depth data were converted from tabular form into the number of minutes for each depth bin for every available 6-h period.

Environmental data

A combination of in situ and remotely sensed environmental data was used to describe the oceanography for this study. In situ potential temperature–depth profiles were obtained from oceanographic vessels and ARGO floats. Two meridional transects were completed during July–August 2005 and March–April 2008. Hydrographic data during the 2005 transect were obtained along the 165°W meridian aboard the Hokkaido University training ship *Oshoro Maru*. Hydrographic data during the 2008 transect were obtained along the 158°W meridian aboard the NOAA Ship *Oscar Elton Sette*. Delayed mode ARGO float profile data were obtained from the Global Ocean Data Assimilation Experiment (GODAE). In situ oceanographic and ARGO data were analyzed and plotted using the Ocean Data View software package.¹

SST data were derived from two data sources. For the years 2003–2005, SST data collected by the 5-channel Advanced Very High Resolution Radiometers (AVHRR)

¹ The free of charge Ocean Data View is available for download at <http://odv.awi.de>.

on board the NOAA-7, NOAA-9, NOAA-11, and NOAA-14 polar orbiting satellites were used. Three-day averages of the raw data on a $9 \text{ km} \times 9 \text{ km}$ spatial resolution were used in this study. AVHRR data were not available for 65 days in 2002, yet AVHRR and data collected from the radiometer sensor onboard the Geostationary Operational Environmental Satellite (GOES) for concurrent temporal periods were analyzed and not found to differ significantly ($r^2 = 0.99$, $P < 0.001$). Three-day running averages of the raw GOES data on a resampled $9 \text{ km} \times 9 \text{ km}$ spatial resolution were then used for the 65 missing days in 2002.

Sea surface height anomaly (SSHA) data mapped at a global $0.3^\circ \times 0.3^\circ$ resolution with orbit error reduction were provided by the Ssalto program of the Centre National d'Études Spatiales, France. This altimetry product is a weekly average of the measured along-track sea level profiles mapped to a Mercator projection. The average of these along-track profiles from 1993 to 1998 was used to create a mean profile that was then subtracted from the mapped product to obtain the sea level anomalies. JASON-1 data from 2002 to 2005 were used in the study. To compute the geostrophic currents, the 1994 NODC World Ocean Atlas Levitus long-term mean 1,000-m dynamic height data set was added to the SSHA files to create an "absolute" SSH. The east–west and north–south gradients were derived from this absolute height and subsequently used to calculate the u (east–west) and v (north–south) components of the geostrophic current, as described in Polovina et al. (1999). Total kinetic energy (TKE) was calculated from the geostrophic components following Stevens and Killworth (1992) using the equation

$$TKE = \frac{1}{2}(u^2 + v^2),$$

where u and v are the geostrophic components as described earlier.

Statistical analysis of dive parameters

Raw dive-frequency data were prepared for statistical analysis using the random deletion technique following Sims et al. (2005). Dive records were randomly deleted for each individual dive parameter to obtain the maximum equal number of 6-h periods for each of the respective dive parameters. Linear regression analysis, Fisher's exact, and nonparametric Wilcoxon rank sum tests were used to compare dive information and environmental data (Snedecor and Cochran 1989).

Ordination techniques were used to classify dive behavior using the maximum dive-depth and dive-duration data. The maximum dive-depth and dive-duration frequency tables were combined, removing one column that contained no positive values (dive-durations >240 min).

The resultant $5,424 \times 23$ matrix was then standardized to mean 0 and standard deviation 1 and introduced to a nonhierarchical K -means cluster analysis [*kmeans* function; stats library, R version 2.81 (R Development Core Team 2008)]. Cluster analyses were repeated 100 times, and the best solution was used based on the smallest value of the sum of within-groups sums-of-squares. Run sets were repeated using a monotonic range of K (centers) (*cascadeKM* function; *vegan* library, R 2.8.1) with the best value of K chosen using the maximum value of the simple structure index. A lower limit of two centers was chosen as a minimum based on previous research that has indicated loggerheads have at least two distinct dive behaviors (Renaud and Carpenter 1994; Houghton et al. 2002; Godley et al. 2003; Polovina et al. 2003). An arbitrary higher limit of 10 centers was chosen as more than 10 clusters would negate any advantages that clustering would offer. The initial peak of the simple structure index occurred at $K = 4$, which indicated that classification of dive type into four clusters was appropriate. These clusters then represented a dive-behavior type for each 6-h period of dive information and are hereafter referred to as dive types C1–C4 throughout the remainder of the text.

Results

Tag results

All 17 deployed tags transmitted data for more than 50 days, with many tags ($n = 6$) transmitting for over 1 year (Table 1). Sixteen of the 17 turtles traveled westward from their capture points, while one turtle moved south-eastward offshore of the BCP before reversing direction and returning to the HLSFG (Fig. 1). Five of the 17 turtles moved across the HLSFG and entered the KEBR region. There was a weak relationship between the size of the animals and the straight-line distance traveled (linear regression: $F_{1,15} = 5.646$, $r^2 = 0.23$, $P = 0.031$). There were no significant differences in tag duration for DH and LH turtles (rank sum test: $W = 31$, $P = 0.673$) or straight-line distances traveled (rank sum test: $W = 38$, $P = 0.884$). Turtles were associated with an SST range of 15.0 – 23.6°C (95% of data) and 95% of the derived speeds were less than 1.75 km h^{-1} (42.1 km day^{-1}).

Overall dive behavior

The pooled percent frequency distributions of dive-depth ($n = 17$), dive-duration ($n = 17$), and time-at-depth ($n = 14$) data for all study regions are presented in Fig. 2. The pooled dive-depth distributions show that more than 85% of the dives were to depths shallower than 5 m, with

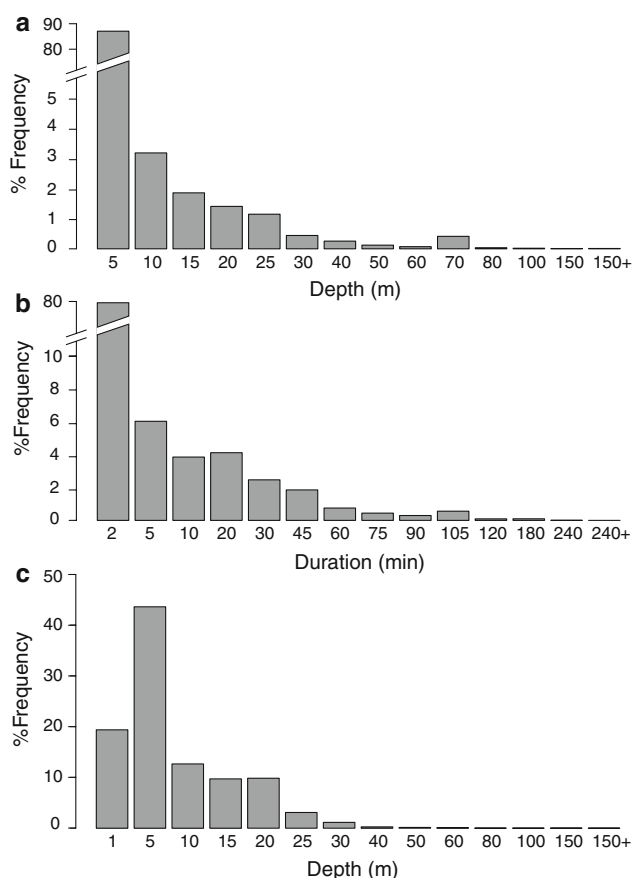


Fig. 2 Frequency distributions of (a) dive-depth (in discrete bins) and (b) dive-duration collected from the 17 SDR tags deployed on juvenile loggerhead turtles in the central North Pacific from 2002 to 2005. Frequency distribution of (c) the time-at-depth for the 14 SDR-16 tags deployed on juvenile loggerhead turtles in the central North Pacific from 2003 to 2005

close to 90% shallower than 15 m (Fig. 2a). Overall, the frequency of dives decreased with depth with the exception of a small mode in the 70 m depth bin that represented 0.6% of total dives. The tags reported 66 dives deeper than 150 m by nine individual turtles. The pooled frequency distribution of the dive-durations show that close to 80% of the dives were less than 2 min in duration, and more than 95% of the dives were shorter than 30 min in duration (Fig. 2b). Similar to the dive-depth distribution, the frequency of dives decreased with duration with the exception of modes in the 20 min and 105 min bins that represented 4.1 and 0.6% of all dives, respectively. Twenty recorded dives by seven individual turtles measured longer than 180 min but no dives measured longer than 240 min in duration. All dives between 180 and 240 min in length occurred during December–March near the STF zone ($SST = 17.3^\circ \pm 1.1^\circ$). The pooled frequency distribution of the time-at-depth shows that turtles spent close to 20% of their time within 1 m of the surface, and more than 85% (95%) of their time shallower than 15 m (20 m) (Fig. 2c).

There was observed variability in the pooled distributions of all three dive parameters over the four 6-h periods of the day. Overall, turtles made significantly more dives during the day than at night (rank sum test: $W = 937,403$, $P < 0.001$), with a slightly larger percentage of dives to depths greater than 15 m during the day (6.1%) than during the night (4.6%). Dive-duration data showed the opposite pattern, with turtles making longer dives during the night than during the day. Additionally, turtles spent more time in the 0–15 m depth range at night (88.9%) than during the day (82.3%).

Dive-type classification

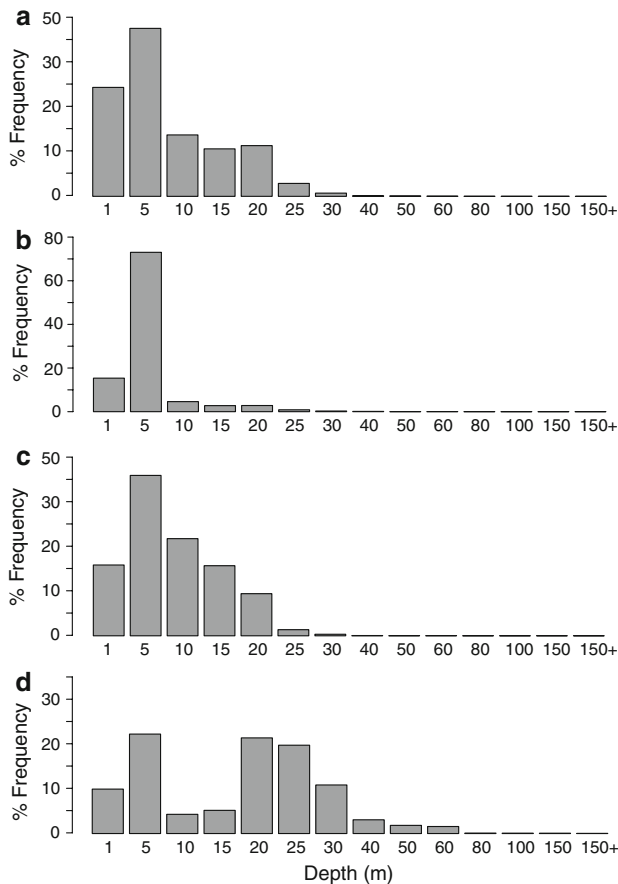
The four distinct dive clusters classified by the cluster analysis are summarized in Table 2 and Fig. 3. Overall, the time-at-depth distributions showed that for C1 dives 61.0% of the time was spent in the 0–5 m depth range, and 15.0% of the time deeper than 15 m (Fig. 3a). C2 dives were very different, with close to 90% of the time spent in the 0–5 m depth range (Fig. 3b). C3 dives were similar to C1 dives, yet with slightly less time in the 0–5 m depth range (51.5%) and deeper than 15 m (11.3%). More time was spent in the 5–15 m depth range for C3 dives (37.3%) than for C1 dives (24.0%). C4 dives represented the 6-h periods with the most time at depths greater than 15 m (58.5%), and the least amount of time in the 0–5 m depth range (32.1%), with a small amount of time spent in the 5–15 m depth range (9.4%, Fig. 3d).

Regional dive behavior: the HLSFG

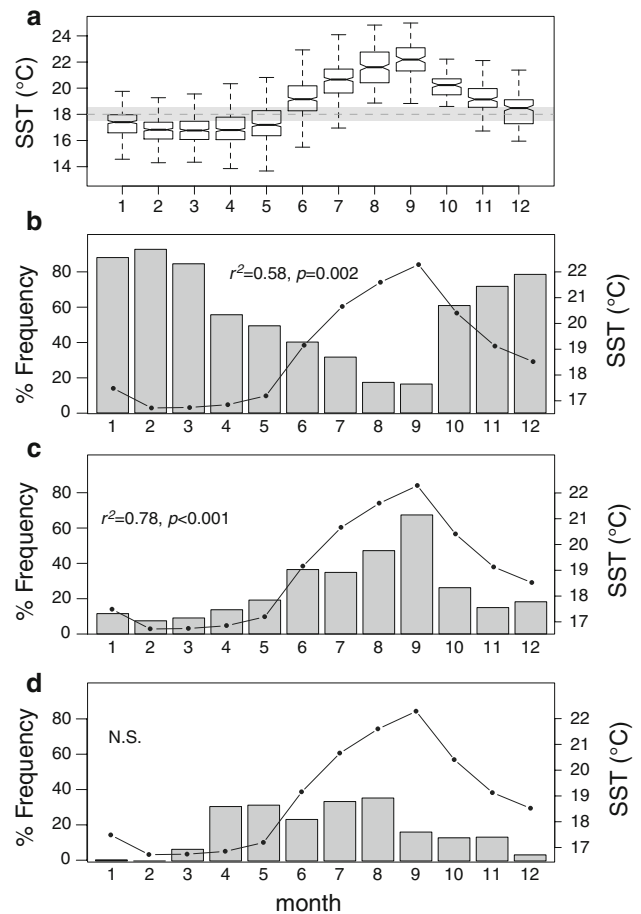
Most of the dive information (78.5%) was collected in the HLSFG, which is currently the main region of interest to the Hawaii-based longline fishery and spatially overlaps the region used by the California-based longline fishery. Three of the four dive classification types (C1–C3) represented 99.5% of the data in the HLSFG region. Turtles in this region were associated with the coldest (warmest) SST during the first (third) quarter of the year, and associated with increasing (decreasing) SST values during the second (fourth) quarters of the year (Fig. 4). The observed seasonal change in SST was a result of the temporal movements of the turtles relative to the latitudinal movements of the NPSTFZ, with the 18°C isotherm here presented as a proxy for this region (Fig. 4). During the first quarter, turtles were located in the colder region of the NPSTFZ. During the second quarter, turtles began to move to the north and transition to the warmer side of the frontal zone. During the third quarter, the turtles were located in the warmest waters and at their farthest point from the 18°C isotherm. Turtles began to travel south during the fourth quarter, yet remained on the warm side of the frontal zone,

Table 2 Mean values and standard errors (in parenthesis) for the number of dives to specific depth bins (top) and of specific duration (bottom) for all 17 loggerheads

Cluster (n)	0–5	6–10	11–20	21–30	31–40	41–50	51–60	61–70	>70
Mean (SE) number of dives to depth bin (m)									
1 (2769)	20.178 (0.399)	1.286 (0.034)	1.383 (0.044)	0.899 (0.037)	0.096 (0.008)	0.038 (0.004)	0.013 (0.002)	0.014 (0.004)	0.025 (0.006)
2 (1261)	123.406 (1.402)	3.01 (0.113)	1.229 (0.066)	0.489 (0.035)	0.078 (0.009)	0.032 (0.005)	0.015 (0.004)	0.069 (0.021)	0.033 (0.01)
3 (1155)	27.813 (0.688)	4.422 (0.133)	6.562 (0.196)	2.327 (0.114)	0.139 (0.014)	0.039 (0.006)	0.012 (0.003)	0.148 (0.031)	0.046 (0.014)
4 (240)	29.879 (2.317)	1.358 (0.136)	1.146 (0.139)	1.733 (0.176)	1.696 (0.112)	1.15 (0.079)	0.783 (0.071)	5.408 (0.25)	0.571 (0.121)
Cluster (n)	0–2	3–10	11–20	21–30	31–45	46–60	60–90	90–105	>105
Mean (SE) number of dives within duration bin (min)									
1 (2769)	17.819 (0.377)	1.65 (0.058)	0.786 (0.026)	0.662 (0.022)	1.26 (0.039)	0.611 (0.021)	0.628 (0.028)	0.237 (0.018)	0.192 (0.016)
2 (1261)	114.48 (1.472)	11.141 (0.281)	1.853 (0.063)	0.601 (0.03)	0.289 (0.02)	0.07 (0.009)	0.049 (0.009)	0.048 (0.015)	0.01 (0.005)
3 (1155)	23.836 (0.654)	7.184 (0.28)	5.922 (0.139)	3.397 (0.093)	0.79 (0.042)	0.067 (0.009)	0.02 (0.006)	0.037 (0.016)	0.001 (0.001)
4 (240)	27.504 (2.277)	4.088 (0.378)	1.521 (0.144)	1.675 (0.148)	2.567 (0.156)	1.096 (0.099)	0.613 (0.105)	3.133 (0.253)	0.013 (0.009)

**Fig. 3** Percent frequency distribution of time-at-depth based on results of the K-means cluster analysis of data on the composite number of dives and dive-duration from the 14 SDR-146 tags for (a) cluster 1, (b) cluster 2, (c) cluster 3, and (d) cluster 4

not transitioning to the cold side until the first quarter. The percent frequency distributions of these dive classifications by month show a seasonal change in dive behavior

**Fig. 4** (a) Box and whisker plots of monthly SST values based on geolocations within the HLSFG region. The dashed horizontal line indicates the 18°C isotherm. The gray box indicates the 17.5–18.5°C temperature range. (b–d) Monthly percent frequency of the dive cluster classifications for (b) dive cluster 1, (c) dive cluster 2, and (d) dive cluster 3 based on all 6-h periods for 17 turtles in the HLSFG region. The solid black lines represent the median monthly SST values for the 17 turtles in the HLSFG region (b–d)

(Fig. 4b–d). During the first quarter of the year, more than 80% of the dives were classified as C1, with a small amount of C3 dives during this time. During the second quarter, the percentage of C1 dives dropped linearly, while the percentages of C2 and C3 dive types increased. The percentage of C2 dives was higher in the third quarter, accounting for more than 67% in September, and C1 and C3 dive types each accounting for 16%. Turtles began to exhibit more C1 dives during the fourth quarter, with more than 78% of this type in December. There was a significant relationship between the monthly percentage of the dives classified as C1 and the median SST, and similarly for C2. Combining C1 and C3 monthly percentages resulted in a more significant relationship with surface temperature ($F_{1,10} = 40.69$, $r^2 = 0.78$, $P < 0.001$).

Meridional transects of temperature are shown to represent the turtle subsurface habitat during March–April (quarters 1–2) and July–August (quarter 3) (Fig. 5a, b). During the first quarter of the year, the subsurface temperature in the area that loggerheads occupy in the North Pacific is well mixed to the depths to which the turtles were diving, with a sharp latitudinal gradient in temperature through the 0–100 m depth range (Fig. 5a). During the third quarter of the year, the region that loggerheads occupy north of $\approx 32^\circ\text{N}$ is highly stratified, with colder temperatures at depth south of the STF, the spatial region that loggerheads occupied at this time of year (Fig. 5b). This change in subsurface conditions is illustrated in the seasonal subsurface temperature–depth profiles collected by ARGO floats in the respective regions that loggerheads occupied during 2003–2005 (Fig. 6a–d). During the first

quarter of the year, the loggerhead habitat was characterized by a well-mixed water column and the coldest surface waters, yet no temperature values dropped below 15°C (Fig. 6a). During the second quarter, the turtle began to migrate to the north, with a thermocline beginning to develop at ≈ 40 m (Fig. 6b). Loggerheads were located at their northern apex during the third quarter, with the habitat characterized by a stratified water column with the warmest surface waters, the shallowest thermocline, and the coldest waters at depth (Fig. 6c). Loggerheads began to travel south during the fourth quarter, and the habitat during this time period was similar to the second quarter, with warm surface waters and a mid-depth thermocline (Fig. 6d).

Regional behavior: the KEBR

Five turtles traveled into the KEBR. All tags for these five individuals ceased transmission while in the KEBR. Three individuals that spent more than 60 days in the KEBR (21128: 65.6 cm; 24644: 56.5 cm; 24645: 66.5 cm SCL) were associated with two anticyclonic warm-core (WC1, WC2) and one cyclonic cold-core (CC1) eddy events (Fig. 7a–i). Turtle 21128 was associated with both WC1 (37 days) and WC2 (44 days), and these associations are described in chronological order. The warm-core eddy WC1 was characterized by higher SSHA values in the center of the eddy and strong, clockwise geostrophic currents. The turtle exhibited a clockwise circular movement pattern, with multiple rotations around the eddy within the highest currents. This was reflected by significantly higher TKE values than the mean background TKE values

Fig. 5 (a) Transect of potential temperature along 158°W during March 26–April 3, 2008, from a cruise of the NOAA Ship *Oscar Elton Sette*. (b) Transect of potential temperature along 165°W during July 29–August 1, 2005 from a cruise of the Hokkaido University training vessel *Oshoro Maru*

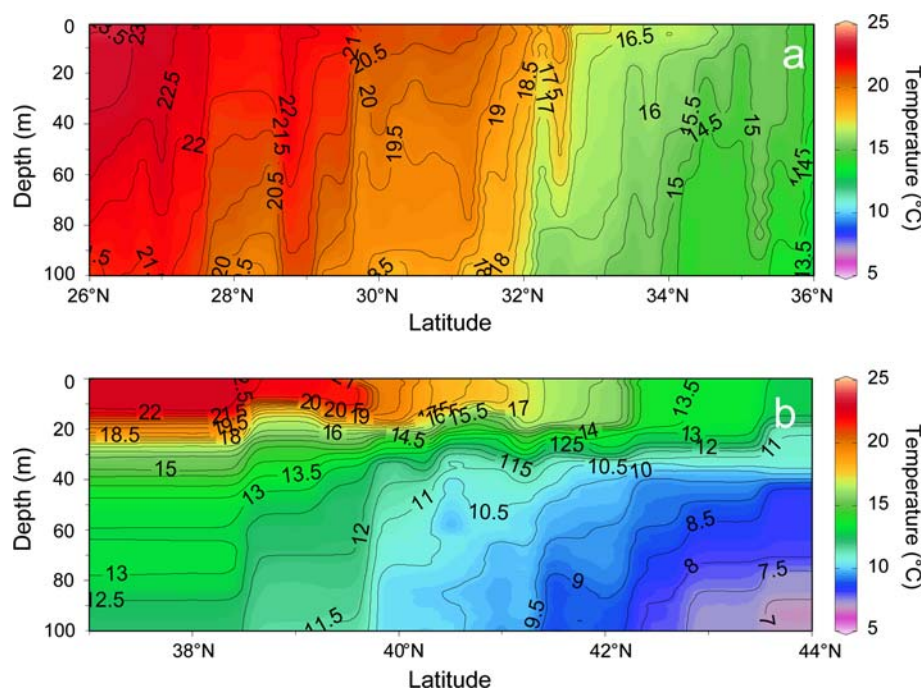
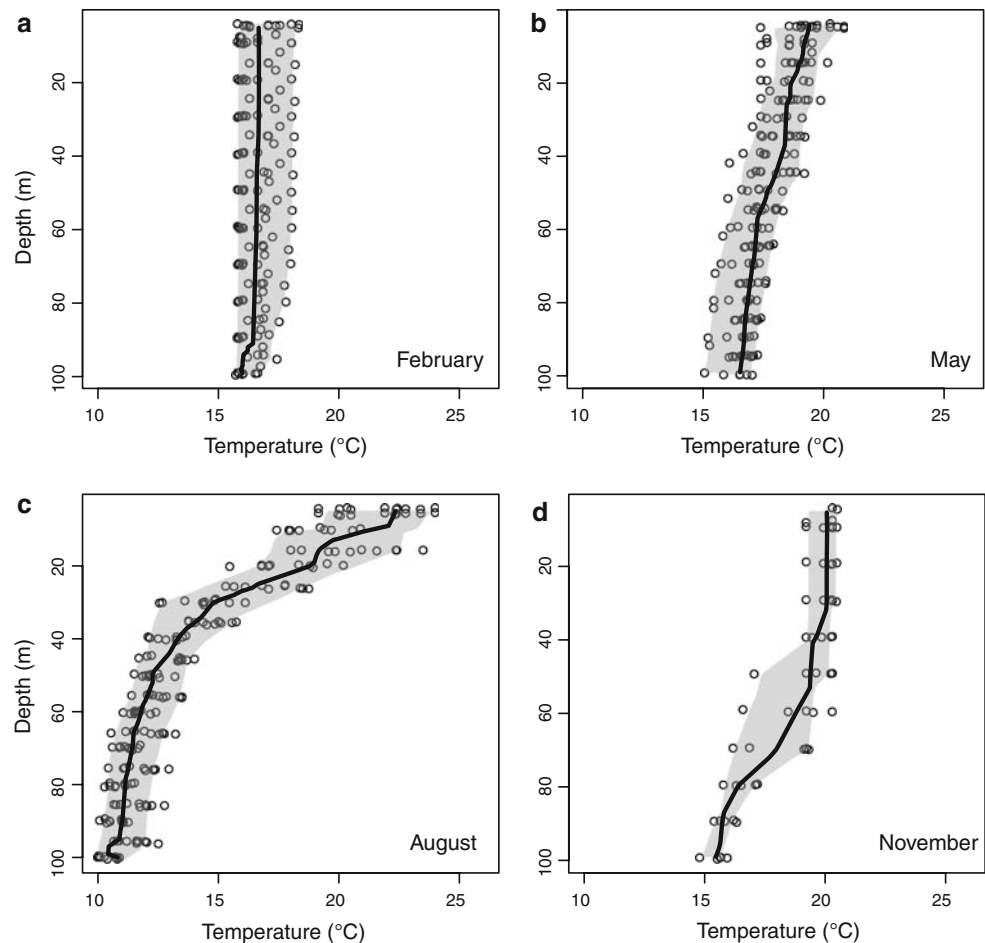


Fig. 6 Temperature–depth profiles collected by ARGO floats in the HLSFG during 2003–2005 for (a) February, (b) May, (c) August, and (d) November. Circles indicate the raw profile data. The solid black lines represent the median temperature value at interpolated depth levels. The shaded areas represent the 95% range of temperature values at interpolated depth levels. Only profiles occurring in the interquartile (25–75%) range of turtle geospatial latitude positions for each respective month were used



(rank sum test: $W = 3,388$, $P < 0.001$) for the WC1 region during this time. Dive behavior outside and associated with the eddy was significantly different (Fisher's exact test: $P < 0.001$), with a decrease in the C2 and an increase in C1 and C4 dive types (Table 3). WC2 was characterized by higher SSHA values and stronger, clockwise surface currents than WC1 (Fig. 7a–c, d–f). Both turtles 21128 and 24644 exhibited clockwise circular movement patterns with multiple rotations within high surface currents while associated with the eddy, yet turtle 24644 (present for 85 days) appeared to travel closer to the edge of WC2 (Fig. 7d–f). Both turtles departed the WC2 region within 7 days of each other at a similar exit point (Fig. 7d–f). TKE values were significantly higher for turtle 21128 (rank sum test: $W = 17,860$, $P = 0.005$) than background TKE values in the WC2 region during the period the turtle was associated with the eddy. Dive behavior was significantly different for turtle 24644 while it was associated with the eddy and after it departed from the eddy (Fisher's exact test: $P < 0.001$). TKE values were not significantly higher for turtle 24644 than background TKE values in the WC2 region (rank sum test: $W = 19,994$, $P = 0.087$). Dive behavior was significantly different for turtle 24644, while

it was associated with the eddy and after it departed from the eddy (Fisher's exact test: $P = 0.041$). Dive behavior of turtle 24644 was also significantly different from the dive behavior of turtle 21128 while both were associated with WC2 (Fisher's exact test: $P < 0.001$) (Table 3). Turtle 24645 was associated for 29 days in 2004 with a cyclonic, cold-core eddy (CC1) formed by a meander in the KEC (Fig. 7g–i). This turtle exhibited a circular, counter-clockwise circular movement pattern, yet only made one rotation during its association with the eddy. The turtle moved around the edge of the eddy within high currents, with TKE values significantly higher than background values during this time (rank sum test: $W = 3,279$, $P < 0.001$) than background values. Turtle 24645 also significantly changed its dive behavior after becoming associated with the cold-core eddy (Fisher's exact test: $P < 0.001$), with close to 60% of its dives classified as C4 during this time; in comparison, about 60% of the turtle's dives were C1 or C3 and 40% C2 when it was not associated with an eddy (Table 3). Comparing the dive behavior for these three turtles associated with eddies shows that the percentage of dive types was similar for three of the four eddy events (Table 3). The C4 dive type

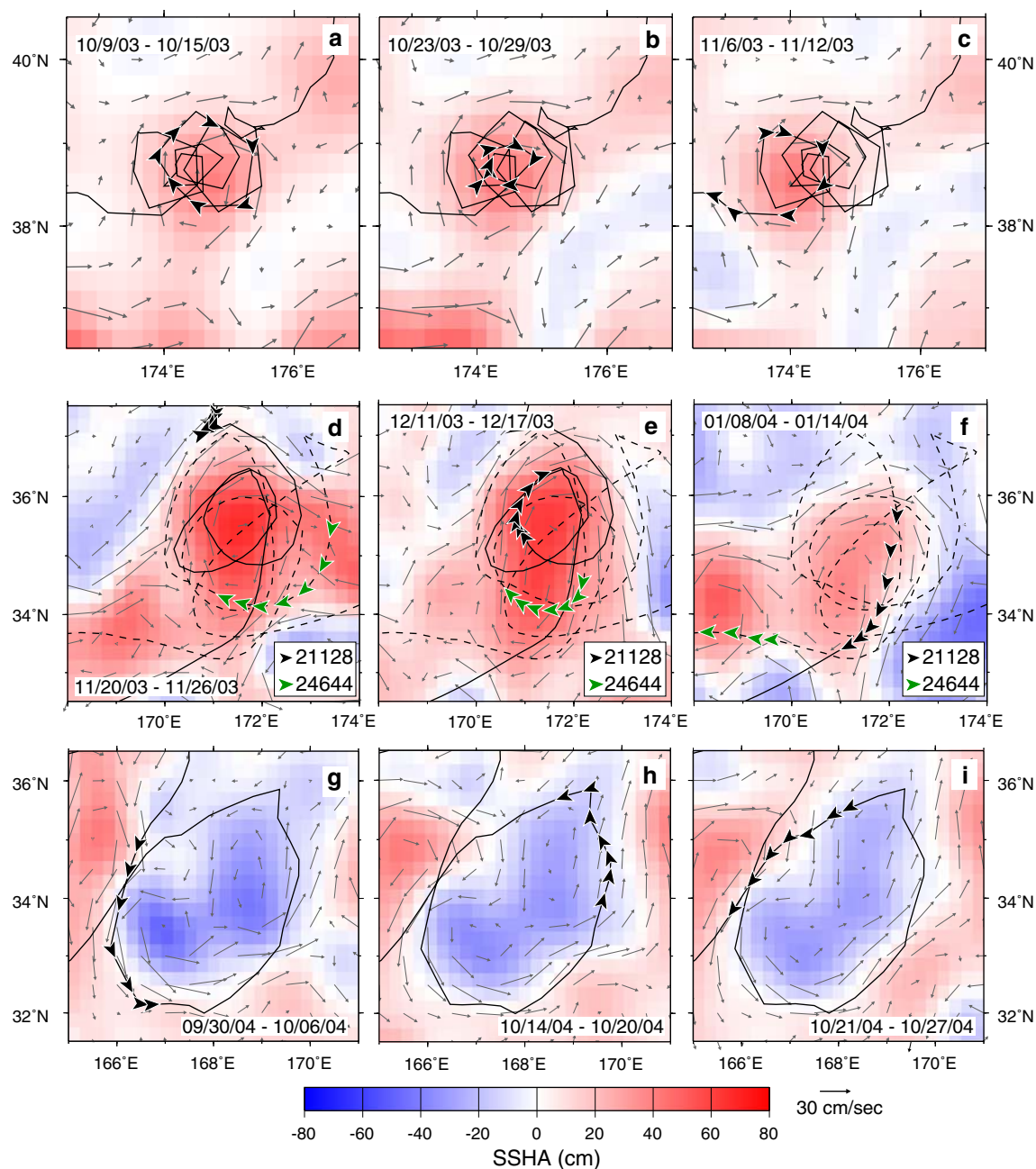


Fig. 7 SSHA (false color) and geostrophic currents (gray arrows) of the region surrounding (a–c) eddy WC1 with geolocations for loggerhead 21128 for October 9–November 12, 2003: (d–f) eddy WC2 with geolocations for loggerheads 21128 (black arrows) and 24644 (green arrows) during November 20, 2003–January 14, 2004:

(g–i) eddy CC1 with geolocations for loggerhead 24645 during September 30–October 27, 2004. The solid and dashed lines represent the full track lines for the complete turtle tracks. Colored arrows represent the geolocations and point in the direction of movement of the turtles during the respective 7-day window

was the most prevalent, with 58–78% classification. Turtle 24644 exhibited a different dive behavior, with 41% (35%) of dives classified as C1 (C2).

Regional behavior: the CC

Only one of the 17 turtles traveled east to the CC region (Fig. 1). This turtle (16129: 61 cm SCL, DH) traveled in a

southeastward direction after its release, traveled close to the pelagic sub-region off the BCP, then traveled in a north-westward direction back to the HLSFG. This return transit took approximately half the time of the southeastern transit, and the median speed during this northwestern transit was significantly higher than during either of the previous two periods (rank sum test: $W = 1,648$, $P < 0.001$; $W = 1706$, $P < 0.001$). The percentage classification of dive types

Table 3 Frequency percentages of dive cluster types for loggerhead turtles not associated (NA) and associated with warm-core (WC) and cold-core (CC) eddy events in the Kuroshio extension bifurcation region

Tag	Area	C1	C2	C3	C4
% of Dive cluster					
21128	NA	3.3	23.3	50	23.3
21128	WC1	20	7.5	2.5	70***
21128	WC2	6.3	15.6	0	78.1***
24644	NA	5.9	58.8	29.4	5.9
24644	WC2	41.9	35.5	16.1	6.5*
24645	NA	19.2	38.5	38.5	3.8
24645	CC1	12.5	12.5	16.7	58.3***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4 Frequency percentages of dive cluster types for loggerhead turtle 16129 during the trip to the California Current (CC) region (HD), while in the CC region near the Baja California Peninsula, and heading away from the CC region (HB)

Tag	C1	C2	C3	C4
% of Dive cluster				
HD	82.7	8.2	5.5	3.6
CC	44.9	8.7	17.4	29
HB	35.5	27.6	23.7	13.2

significantly changed during these three transit periods (Fisher's exact test: $P < 0.001$) (Table 4). The C1 dive type was the most prevalent for all three periods, yet the amount of C2–C4 dive types changed based on the transit region (Table 4). A decrease (increase) in the percentage of C1 (C4) dive types occurred after the animal crossed the 120°W meridian, with only a small percentage of C2 and C3 dive types during this period. An apparent change in dive behavior occurred during the northwestern transit west of 120°W, with a 15–20% increase in the percentage of C2 and C3 dive types during this time.

Discussion

The combined dive records from the 17 turtles in this study showed that more than 80% of the dives occurred to depths less than 5 m, with more than 60% of the turtles' time spent in this depth range. This compares well to the reported dive behavior for two individual loggerheads captured by the longline fishery in the North Pacific, where 90% of the dives occurred to depths less than 5 m, with most of the time spent shallower than 40 m for both day and night (Polovina et al. 2003, 2004). Diel variability in the dive parameters was observed between the four 6-h periods of the day, with turtles making significantly more

dives, and dives of shorter duration, during the day than at night. This diel behavior was observed in loggerheads both in the Gulf of Mexico and in the Mediterranean Sea (Renaud and Carpenter 1994; Godley et al. 2003) and was hypothesized to reflect resting (active) behavior during the night (day) (Godley et al. 2003). Results from the cluster analysis of dive information showed that turtles exhibited four distinct dive behaviors during this study. Houghton et al. (2002) generalized six distinct dive types based on the previous dive studies of loggerhead and green turtles (Minamikawa et al. 1997; Hochscheid et al. 1999; Hays et al. 2000). Five of these six dive types were similar, and were conducted to greater depths than the sixth dive type, which represented a more surface-oriented behavior. The C1, C3, and C4 dive types all represented behaviors where turtles made fewer overall dives, yet to greater depths and for longer durations. While each of these dive types was similar in this regard, there were differences in the dive depths and durations between them. This behavior is similar to foraging dives as described in the literature; foraging is thought to be linked to an increased number of dives and a strong inverse relationship between the number of dives and dive-durations (Renaud and Carpenter 1994; Godley et al. 2003).

The C2 dive type was most different from the other three types and represents 6-hour periods when turtles made numerous short dives to shallow depths. The C2 dive type is most likely a combination of transit and shallow-foraging dive behavior. Previous studies have also reported these two differences in dive behavior, with an inverse correlation observed between the number and duration of dives (Renaud and Carpenter 1994) as well as diel patterns in dive-durations (Godley et al. 2003).

Several recent studies have used tag information to address the important issue of incidental mortality of sea turtles hooked in longline fisheries (Chaloupka et al. 2004; Sasso and Epperly 2006; Swimmer et al. 2006). In our study, there was no statistical difference in tag duration between the DH and LH turtles. Cessation of tag transmissions may be attributed to several factors, including electronic failure, detachment, or a possible mortality event (Hays et al. 2007). Results from a post-release mortality study of tagged immature loggerheads captured in the Hawaii-based pelagic longline fishery indicated that the survival functions for LH and DH turtles were only different within the first 90 days post-release (Chaloupka et al. 2004). They are conservative in describing these results as an upper bound on the apparent level of loggerhead mortality for the two hooking type groups of turtles as there are multiple reasons for transmission failure (Hays et al. 2007). However, even if the survival function of Chaloupka et al. (2004) is used, only one tag in this study ceased transmission in less than 90 days. This turtle

(44362) was indeed deeply hooked, yet without additional information we are hesitant to speculate whether cessation of transmission was caused by a mortality event or tag failure from other causes. Additionally, three of the five longest transmission periods were observed on tags affixed to deeply hooked animals. Future studies to address this important issue will hopefully benefit from the additional satellite tag information recorded by the satellite tag to determine when and why transmitters fail (Hays et al. 2007).

Regional dive behavior: the HLSFG

There was seasonal variability in the spatial location and dive behavior of the 17 loggerheads within the HLSFG region. Loggerheads spent the majority of their time in the 0–5 m range throughout the year, yet there were changes in the number and duration of dives possibly reflecting oceanographic conditions. During the first quarter, loggerheads occupied cooler waters to the north of the STF. A deep mixed layer characterized this region of the North Pacific during this time, with surface temperatures being a strong proxy for subsurface temperatures down to 100 m. More than 80% of the loggerhead dive behavior during this time was classified as C1 type behavior, which reflected deeper dives of longer duration. This was observed in the time-at-depth for this season, when more than 15% of the time was spent deeper than 15 m. The increase in the depth and duration of these deeper dives during this period is most likely a result of the oceanography. An increase in surface winds in this region in the first quarter results in a deeply mixed surface layer that may distribute non-surface oriented prey more evenly throughout the water column. Stomach content analysis showed that juvenile North Pacific loggerheads are opportunistic feeders that ingest items floating on or near the surface (e.g., *Carinaria cithara*, *Pyrosoma* spp., *Janthina* spp., *Velella velella*) but also take advantage of other prey items throughout the water column when available (Parker et al. 2005).

In our study, turtles began to move to the north during the second quarter in apparent response to the seasonal movement of the NPTZ. The temperature–depth profiles reflect this spatiotemporal movement, with turtles inhabiting warmer surface waters with a shallower thermocline. A change in dive behavior with a 20% shift from C1 to C3 dive types occurred during this time. The C3 dive type was characterized by a greater number of slightly shorter dives to depths shallower than the C1 dive type, which may reflect a shallowing of the thermocline during this period and a vertical movement in the aggregation of subsurface prey at depth. The larger percentage of C2 dive types occurred when turtles were at their northernmost locations in the third quarter of the year. During this time, the region

is characterized by the warmest surface and coldest subsurface waters encountered. A sharp thermocline at shallow depths results in temperatures of less than 15°C at ≈ 20 m. Turtles exhibited the shallowest dive behavior in this period, with an increase in the C2 dive types characterized by the greatest number of dives per day to shallow depths. Shorter dives have been reported for transiting loggerhead turtles in the Mediterranean (Godley et al. 2003), but here may instead reflect the shallow aggregation of subsurface prey items as a result of the increased stratification in the water column. Similar to the observed decrease in C1 dive types during the second quarter, there was an increase in the percentage of C1 types in the fourth quarter. Temperature–depth profiles from this period are similar to those from the second quarter, yet with a more defined thermocline. An observed increase in the percentage of C2 dives may reflect a continuation of available prey in the surface waters, an increase in transit behavior by the animals or a combination of these factors.

Temperature data were not collected by the satellite tags, yet can be inferred from the dive information and the temperature–depth profiles during this time. There has been postulation of thermal niches for leatherback and loggerhead turtles (Hays et al. 2002; McMahon and Hays 2006), with loggerheads showing an internal thermal dependence on ambient temperatures that is stronger in smaller turtles (Sato et al. 1998). It has been stated that the 15°C isotherm may represent a thermal boundary for leatherbacks and loggerheads (McMahon and Hays 2006; Brazner and McMillan 2008). This could possibly be more a thermal preference than a limit, as turtles have been observed to make dives corresponding to temperatures less than 15°C (Hochscheid et al. 2007, PIFSC, unpublished data). However, there is an observed importance of the 15°C isotherm which is also indicated by our study. More than 99% of the turtle's time was spent in depths corresponding to temperatures warmer than 15°C with the turtles altering their dive behavior to shallower (deeper) depths seasonally as the thermocline shoaled (dropped). More information is necessary to define whether this change in behavior is based on a vertical shift in prey resulting from increased stratification of the water column during this time or based on thermal limitations or preferences.

Regional dive behavior: the KEBR

Five of the 17 animals in this study traveled through the HLSFG to the KEBR, with three tags transmitting more than 60 days within the latter region. It is difficult to ascertain exactly why those five particular turtles traveled to the KEBR. Size did not appear to be the primary factor, as these were not the five largest turtles in this study, and three of them were of the median size. It is more probable

that a combination of release location and time at liberty were important factors. The times at liberty for all five turtles were above the median value, with three in the upper quartile. Previous results from tracking studies have shown turtles moving west travel to this region (Polovina et al. 2006), allowing us to infer that longer times at liberty for tags may have resulted in more animals entering this region. Without additional data, however, this is purely speculative.

The three tags that transmitted information in the KEBR for more than 60 days indicated that turtles were associated with mesoscale eddies, at times in temporal succession. The track from one of these turtles, in addition to other examples of the use of mesoscale features, was reported in Polovina et al. (2006). Here, additional track information coupled with dive information are added to expand on turtle behavior in this region. These tracks indicated that two of the three turtles were associated with the strongest currents in both warm-core and cold-core mesoscale events. However, turtle 24644, which was reported in Polovina et al. (2006), was in the same feature as turtle 21128 yet was not associated with stronger-than-background currents. The dive behavior of these turtles appeared to indicate eddy usage; deeper, longer dives were associated with stronger currents in the eddy. Turtle 24644 remained within weaker surface currents while associated with the eddy and spent a greater percentage of time diving to shallower depths for shorter durations. This individual was smaller than the other two turtles, yet with this sample size it is difficult to draw conclusions based on morphological differences. As the main prey of loggerheads are surface-oriented and aggregated in convergent areas (Parker et al. 2005), the use of the edges of warm-core eddies was unanticipated, yet this behavior may be more directed by physics than biology. The highest currents in this study were associated with the edges of both eddy types, yet surface convergence occurs in different areas for warm-core and cold-core events. We would expect the highest surface convergence in the center or edge of a warm- or cold-core eddy, respectively. In a warm-core eddy, the physiological advantages of energy conservation given by the areas of high currents (edges) may outweigh any possible biological disadvantages. The appearance of a higher amount of C4 dive-type behavior by two of the three turtles may be a result of a combination of the use of the highest currents for transit with the ability to dive deeper based on warmer subsurface conditions. Temperature data collected by ARGO profiling floats in this region show that subsurface temperatures down to 100 m are warmer in this region than in the HLSFG during these times (not shown). This may enable the turtles to conduct deeper, longer, C4 type dives in this region, a behavior rarely observed in the HLSFG where subsurface temperatures are much colder. It

may also be possible that sessile organisms are constrained to the edges of the eddy, as a submergence of organisms in the center of a warm-core eddy may result in a spread to the edges. Turtle 24644 did not occupy the region with the highest surface currents; however, it occupied the edge of the eddy at a distance farther from the center than turtle 21128. This may imply that placement within the eddy edge can affect the dive behavior of turtles. The physiological explanation is also supported by the observation that turtles occupied areas of both warm-and cold-core eddies with the highest currents, rather than the areas where the greatest surface convergence would occur. Residence time within the eddies, however, suggests that while dive behavior is similar for both warm-core and cold-core events, turtles spend less time within cold-core events than warm-core eddies (Polovina et al. 2006). Additional information on loggerhead prey and additional dive information from more individuals would allow for a clearer explanation of observed dive behavior in this region. Future studies may also compare tag-derived dive behavior tag data from this area with other oceanic regions to understand whether the eddy associations observed here are general or localized behavior.

Regional dive behavior: the California Current region

One turtle (16129) in this study traveled southeast to the California Current region near the BCP. Caution should be exercised not to over interpret results based on one animal, yet this was one of the very few loggerheads we have seen travel this far east after capture in the oceanic phase. Loggerheads of similar size are reported in numbers and, based on satellite telemetry results, spend considerable time in this region (Peckham et al. 2007). There is insufficient information to determine why this particular individual traveled east. Turtle size may be important in determining both the initial transit to the CC region and subsequent return to the HLSFG. Turtle 16129 was not the largest in the study (61 cm SCL), yet was in the upper quartile of the SCL ranges. However, its size was significantly less than the mean size of turtles tracked in a previous study in this area (Peckham et al. 2007).

Additionally, turtle 16129 did not remain off the BCP, a region that has been shown to be a high use foraging and developmental area for large numbers of juvenile loggerheads originating in Japan after their initial oceanic phase in the North Pacific (Bowen et al. 1995; Peckham et al. 2007). None of the juvenile loggerheads tagged off the BCP in previous studies have been observed to move north from this region (Peckham et al. 2007, Dutton, NMFS, unpublished data), and it is generally thought that oceanic juveniles settle into the BCP foraging area where they take up long-term residence before migrating back to inhabit the

neritic areas near their natal beaches in Japan. Furthermore, none of the loggerheads tracked in our study, as well as previous studies in the North Pacific have traveled to and remained in the BCP region for any length of time (Polovina et al. 2000, 2004, 2006; Kobayashi et al. 2008). Additional study of loggerheads is required to understand the transition between the oceanic phase and site fidelity at the BCP region.

Changes in turtle 16129's dive-behavior were observed as it traveled through the three study-defined subregions within the CC region. The transit speed and dive behavior exhibited by the turtle were very different during the southern and eastward transect than during the return transect. The dive type classifications made by the cluster analysis reflected this, with more C1 and C4 dive types present during these first two transects. Turtle behavior was similar to prior behavior on the initial return transect, yet once it crossed the 120°W meridian the turtle abruptly altered its behavior, with an increase in speed and more C2 and C3 dive behavior recorded. The change in dive behavior to these shallower dive behaviors is most likely correlated to the increase in speed, with the C2 dives representing the transit dives made by the turtle. These results indicate a potential change in dive behavior by turtles in this subregion that should be further investigated.

Biological and conservation implications

One aim of this study was to understand the potential use of loggerhead dive information to minimize fishery bycatch. The majority of loggerhead bycatch by the Hawaii-based longline fishery occurs north of Hawaii during January–March and is associated with a very specific thermal range of 17.5–18.5°C (Howell et al. 2008). Our results indicate that there was seasonal variability in the dive behavior within the HLSFG, with deeper, longer dives during the first quarter of the year. Additionally, the longest recorded dives (>180 min) occurred during December to March, the time of year when historically most of the loggerhead bycatch has occurred. Eighty percent of the 6-h periods were classified as C1 during this period, representing a potential overlap in the vertical distribution of the turtles and the shallow set fishing gear. Recent time–depth recorder studies indicate that shallow set longline gear tends to be set deeper than 15 m (Hawn, NMFS, personal communication). Our data confirm that more than 90% of the turtle's time was spent shallower than 15 m in the HLSFG during the first quarter of the year; however, the amount of time that turtles do spend deeper than 15 m may be important to consider. For example, the dive data from these 17 turtles indicate that placement of longline fishing gear in depths below 25 m should avoid the shallower region of the water column where turtles appear to spend 99% of their time on

average. Any change in the depth of the gear must be balanced with the ability of a hooked turtle to reach the surface and breathe, yet setting gear slightly deeper may further minimize potential interactions between loggerheads and longline fishing gear. This increased amount of time at depths where longline gear occurs in this region may explain why increased bycatch by longline fisheries occurs in a specific thermal range during the first quarter of the year.

Additionally, this new information on dive behavior will enhance existing spatial models of loggerheads based on tracking data (Kobayashi et al. 2008) and reported bycatch (Howell et al. 2008). The models may be used to predict areas where loggerheads are more likely to occur both in horizontal and vertical space. An improved ability to predict should increase our ability to provide information on loggerhead essential habitat, probability of fishery interactions, and ultimately bycatch reduction in the longline fishery.

Results from this and previous studies have shown that seasonally shifting oceanographic features and dynamic hotspot areas are important habitats for juvenile loggerheads during the pelagic phase of their life cycle in the North Pacific (Polovina et al. 2000, 2004, 2006; Kobayashi et al. 2008). Analysis of the tag-derived dive information has revealed that there is spatial and temporal variability in dive behavior that was associated with these large- and meso-scale features. Additionally, the tag information indicates that their dive behavior varies depending on the oceanographic system with which they are associated. These results increase our understanding of the ecological dynamics of juvenile loggerheads during their important oceanic phase in the North Pacific Ocean.

Acknowledgments The authors wish to thank Michael Seki, Reka Domokos, Donald Kobayashi, Kyle Van Houtan, Steven Bograd, Daniel Palacios, T. Todd Jones, and Pierre Kleiber for fruitful discussions and comments regarding this manuscript. We also wish to thank Don Petersen, Lyle Enriquez, and the fisheries observers with the NOAA Fisheries Service Southwest Regional Office in Long Beach, CA for deployment of the transmitters and providing associated information on the bycaught turtles, the captain and crew of both the NOAA research vessel *Oscar Elton Sette* and the Hokkaido University Training Ship *Oshoro Maru* including professors Kenshi Kuma, John Bower, Hiroji Onishi, and Atsushi Yamaguchi, and students from Hokkaido University and Hidetada Kiyofuji who aided in the collection of the in situ data temperature data. The first author also wishes to thank Sei-Ichi Saitoh for assistance with this project. Altimetry data used in this study were produced by the Ssalto program and obtained from Collecte Localisation Satellites (CLS) center under the auspices of the Centre National d'Études Spatiales of France (CNES). SST data were processed and distributed by the NESDIS OceanWatch Central Pacific Node. This research was conducted as part of the NOAA Fisheries and the Environment (FATE) program and was partially supported by the National Aeronautics and Space Administration through a grant provided by the Applied Sciences Program in the Earth Science Division.

References

- Alfaro Shigueto J, Mangel J, Seminoff J, Dutton P (2008) Demography of loggerhead turtles *Caretta caretta* in the southeastern Pacific Ocean: fisheries-based observations and implications for management. *Endanger Species Res* 5:129–135
- Alfaro-Shigueto J, Dutton PH, Mangel J (2004) First confirmed occurrence of loggerhead turtles in Peru. *Mar Turt Newsl* 103:7–11
- Bailey H, Shillinger G, Palacios D, Bograd S (2008) Identifying and comparing phases of movement by leatherback turtles using state-space models. *J Exp Mar Biol Ecol* 356:128–135
- Balazs GH, Pooley SG, Murakawa SK (1995) Guidelines for handling marine turtles hooked or entangled in the Hawaii longline fishery: results of an expert workshop held in Honolulu, Hawaii March 15–17, 1995. NOAA Tech Memo NMFS NOAA-TM-NMFS-SWFSC-222 46 pp
- Balazs GH, Miya RK, Beavers SC (1996) Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath JA, Bernard DE, Mubick JA, Bell BA (comps) Proceedings of the 15th annual symposium on sea turtle biology and conservation, p 21–26. US Department of Commerce, NOAA Tech Memo NMFS/SWFSC-37
- Bentivegna F (2002) Intra-Mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. *Mar Biol* 141:795–800
- Bograd SJ, Foley DG, Schwing FB, Wilson C, Laurs RM, Polovina JJ, Howell EA, Brainard RE (2004) On the seasonal and interannual migrations of the transition zone chlorophyll front. *Geophys Res Lett*, pp L17,204.1–L17,204.5
- Bowen BW, Karl SA (2007) Population genetics and phylogeography of sea turtles. *Mol Ecol* 16(23):4886–4907
- Bowen B, Abreu-Grobois F, Balazs G, Kamezaki N, Limpus C, Ferl R (1995) Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proc Natl Acad Sci USA* 92:3731–3734
- Boyle MC, FitzSimmons NN, Limpus CJ, Kelez S, Velez-Zuazo X, Waycott M (2009) Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. *Proc Royal Soc B* 276(1664):1993–1999
- Brazner JC, McMillan J (2008) Loggerhead turtle (*Caretta caretta*) bycatch in Canadian pelagic longline fisheries: Relative importance in the western North Atlantic and opportunities for mitigation. *Fish Res* 91(2–3):310–324
- Chaloupka M, Parker P, Balazs G (2004) Modelling post-release mortality of loggerhead sea turtles exposed to the Hawaii-based pelagic longline fishery. *Mar Ecol Prog Ser* 280:285–293
- Dodd CK, Byles R (2003) Post-nesting movements and behavior of loggerhead sea turtles (*Caretta caretta*) departing from east-central Florida beaches. *Chelonian Conserv Biol* 4(3):530–536
- Donoso M, Dutton PH (2008) Numbers, distribution and stock origin of sea turtles caught incidentally in the Chilean longline fishery for swordfish, 2001–2002. NOAA Tech Memo NMFS SEFSC 567:15–16
- Godley BJ, Broderick AC, Glen F, Hays GC (2003) Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking. *J Exp Mar Biol Ecol* 287(1):119–134
- Hatase H, Omuta K, Tsukamoto K (2007) Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *J Zool* 273(1):46–55
- Hays GC, Adams CR, Broderick AC, Godley BJ, Lucas DJ, Metcalfe JD, Prior AA (2000) The diving behaviour of green turtles at Ascension Island. *Anim Behav* 59:577–586
- Hays GC, Broderick A, Glen F, Godley B, Houghton J, Metcalfe J (2002) Water temperature and interesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. *J Therm Biol* 27(5):429–432
- Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags deployed on marine animals stop transmitting? *J Exp Mar Biol Ecol* 349:52–60
- Hochscheid S, Godley BJ, Broderick AC, Wilson RP (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Mar Ecol Prog Series* 185:101–112
- Hochscheid S, Bentivegna F, Bradai MN, Hays GC (2007) Overwintering behaviour in sea turtles: dormancy is optional. *Mar Ecol Prog Series* 340:287–298
- Houghton JDR, Broderick AC, Godley BJ, Metcalfe JD, Hays G (2002) Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Mar Ecol Prog Ser* 227:63–70
- Howell EA, Kobayashi DR, Parker D, Balazs GH, Polovina J (2008) Turtlewatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger Species Res* 5:267–278
- Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Mar Ecol Prog Ser* 337:255–264
- Kamezaki N, Matsui M (1997) A review of biological studies on sea turtles in Japan. *Jpn J Herpetol* 17:16–32
- Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodoma J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Sugunuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I (2003) Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington, DC, pp 210–217
- Kobayashi DR, Polovina JJ, Parker DM, Kamezaki N, Cheng I, Uchida I, Dutton P, Balazs GH (2008) Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): insights from satellite tag tracking and remotely sensed data. *J Exp Mar Biol Ecol* 356:96–114
- McCracken ML (2004) Modeling a very rare event to estimate sea turtle bycatch: Lessons learned. NOAA Tech Memo NMFS-PIFSC-3; 25 p
- McMahon C, Hays G (2006) Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob Change Biol* 12(7):1330–1338
- Minamikawa S (2000) Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J Exp Biol* 203(19):2967–2975
- Minamikawa S, Naito Y, Uchida I (1997) Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *J Ethol* 15(2):109–118
- Parker DM, Cooke W, Balazs GH (2005) Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific. *Fish Bull* 103:142–152
- Peckham S, Diaz D, Walli A, Ruiz G, Crowder L, Nichols W (2007) Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS One* 10:e1401
- Pickard GL, Emery WJ (1990) Descriptive physical oceanography: an introduction, 5th edn. Pergamon Press, Oxford
- Polovina JJ, Kleiber P, Kobayashi DR (1999) Application of TOPEX/POSEIDON satellite altimetry to simulate transport dynamics of the spiny lobster (*Panulirus marginatus*) in the Northwestern Hawaiian Islands. *Fish Bull* 97:132–143
- Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs G (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish Oceanogr* 9:71–82

- Polovina JJ, Howell E, Kobayashi DR, Seki MP (2001) The Transition Zone Chlorophyll Front, a dynamic global feature defining migration and forage habitat for marine resources. *Prog Oceanogr* 49:469–483
- Polovina JJ, Howell E, Parker DM, Balazs GH (2003) Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) turtles in the central North Pacific: might deep longline sets catch fewer turtles? *Fish Bull* 101:189–193
- Polovina JJ, Balazs GH, Howell EA, Parker DM, Seki MP, Dutton PH (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish Oceanogr* 13(1):36–51
- Polovina JJ, Uchida I, Balazs GH, Howell EA, Parker D, Dutton P (2006) The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Res Part II* 53(3–4):326–339
- Qiu B (2001) Kuroshio and Oyashio Currents, Academic Press, pp 1413–1425
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Renaud ML, Carpenter JA (1994) Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bull Mar Sci* 55(1):1–15
- Roden G (1972) Temperature and salinity fronts at the boundaries of the Subarctic-Subtropical Transition Zone in the western Pacific. *J Geophys Res* 27:7175–7187
- Roden G (1980) On the Subtropical Frontal Zone north of Hawaii during winter. *J Phys Oceanogr* 10:342–362
- Roden G (1991) Subarctic-subtropical transition zone of the North Pacific: large-scale aspects and mesoscale structure, In: Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone. In: Wetherall J (ed) NOAA Technical Report 105
- Sakamoto W, Uchida I, Naito Y, Kureha K, Tujimura M, Sato K (1990) Deep diving behavior of the loggerhead turtle near the frontal zone. *Nippon Suisan Gakkaishi* 56(9):1435–1443
- Sasso CR, Epperly SP (2006) Survival of Pelagic Juvenile Loggerhead Turtles in the Open Ocean. *J Wildl Manage* 71:1830–1835
- Sato K, Sakamoto W, Matsuzawa Y, Tanaka H, Naito Y (1994) Correlation between stomach temperatures and ambient water temperatures in free-ranging loggerhead turtles, *Caretta caretta*. *Mar Biol* 118(2):343–351
- Sato K, Matsuzawa Y, Tanaka H, Bando T, Minamikawa S, Sakamoto W, Naito Y (1998) Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. *Can J Zool* 76:1651–1662
- Seki MP (2003) Physical characterization of and biological responses at large- and meso-scale oceanographic phenomena in the Subtropical North Pacific. Ph.D. thesis, Hokkaido University
- Seki MP, Polovina JJ, Kobayashi DR, Bidigare RR, Mitchum GT (2002) An oceanographic characterization of swordfish (*Xiphias gladius*) longline fishing grounds in the springtime subtropical North Pacific. *Fish Oceanogr* 11(5):251–266
- Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J Anim Ecol* 74:755–761
- Snedecor G, Cochran W (1989) Statistical methods, 8th edn. Iowa State University Press
- Stevens DP, Killworth PD (1992) The distribution of kinetic energy in the Southern Ocean: A comparison between observations and an eddy resolving general circulation model [and discussion]. *Philos Trans R Soc London B* 338:251–257
- Swimmer Y, Arauz R, McCracken ML, McNaughton L, Ballesterio J, Musyl M, Bigelow KA, Brill RW (2006) Diving behavior and delayed mortality of olive ridley seas turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Mar Ecol Prog Ser* 323:253–261